Advantages of Hopping on a Zig-zag Course

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Abstract

We investigate self-moving particles which prefer to hop with a certain turning angle equally distributed to the right or left. We assume this turning angle distribution to be given by a double Gaussian distribution. Based on the model of Active Brownian particles and we calculate the diffusion coefficient in dependence on the mean and the dispersion of the turning angles. It is shown that bounded distribution of food in patches will be optimally consumed by the objects if they hop preferably with a given angle and not straight forwardly.

Key words: Active motion, self-propelled particles, vortex motion, turning angle, Zooplankton

1 Introduction

In 1827, when the British botanist Robert Brown discovered the erratic motion of small particles immersed in a liquid, he considered them first as living entities. Later on Einstein and Smoluchowski [1] have shown that the behavior of Brownian particles are due to the molecular agitation, i.e. collisions from the side of the solvent molecules only.

The most fascinating formulation was given by Paul Langevin [2] who added random forces to the equation of motion, in addition to the viscous forces acting on the particles in the fluid. Recently, this latter formulation was used to study active particles which are self-moving particles thanks to some energy supply and, thus, remember the entities as they were considered by Brown. This concept of active Brownian particles is easy, negative friction at smaller

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velocities resembles a pump of energy. This energy is transformed into kinetic one up to some velocity (for higher ones, dissipation wins again) and the particles starts to be moving along their given direction. In case of additionally acting forces, in particular random ones, the individuals change the direction as well as the modulus of their velocity.

Several interesting phenomena were studied in the past. Simple models of active particles were studied already in many earlier works [3–6]. For broader reviews one might refer to [7–9]. Other previous versions of Active Brownian particle models [10,11] consider more specific activities, such as environmental changes and signal–response behavior. In these models, the Active Brownian particles (or active walkers, within a discrete approximation) are able to generate a self-consistent field, which in turn influences their further movement and physical or chemical behavior. This non-linear feedback between the particles and the field generated by themselves results in an interactive structure formation process on the macroscopic level. Hence, these models have been used to simulate a broad variety of pattern formations in complex systems, ranging from physical to biological and social systems [10, 12, 13].

The concept of Active Brownian particles was also applied to the motion of small water flees, so called *Daphnia* [9, 14] where it can also explain some collective swarming and curling of the animals and in light shafts [15, 16]. These *Daphnia* exhibit another property during their motion as was recently detected in measurements [15]. During a small time step they hop with some preferred angle to the left or right of their previous motion. Hence the direction of motion is due to some given distribution of turning angles which determines the preferred direction after the time step.

In [17] we applied a random walk model to find the effective diffusion coefficient of the random motion with preferred turning angles. For this purpose we have used and expression derived by Kareiva and Shigesada (see [18] for details) and applied it to the experimental observations [15]. Here we develop a continuous model which is based on the stochastic equations of motion in two dimensions. Again we find a decrease of diffusion with the mean turning angle and a non-monotonous dependence on the dispersion of angles.

In addition we let the particle consume some non-moving food with constant rates. If this food is distributed in bounded regions, it would be suggestive to hop with a preferred turning angle. That's why the food consumption in a given time is maximized as will be shown in the last section.

2 Equations of motions of Active Brownian particles

The heart of Active Brownian particles is an energy pump modeled by negative dissipation at small velocities. Thus we suppose that the relaxation coefficient of the velocities is negative for small velocities. For large velocities dissipation again overwhelms. A good prototypical choice goes back to Rayleigh who considered first nonlinear friction as [19]

$$\gamma(v) = -\alpha + v^2 \tag{1}$$

where v is the modulus of the velocity-vector. This type of friction function describes a source of energy if $v^2 < \alpha$ and lowers the velocity in the opposite case. This is done upto a stationary velocity which has the absolute value of $\sqrt{\alpha}$.

Since *Daphnia* hop in first approximation in a two dimensional plane we assume that the position and the velocities are determined by the equations of motion:

$$\frac{\mathrm{d}\vec{r}}{\mathrm{d}t} = \vec{v}\,, \qquad \frac{\mathrm{d}\vec{v}}{\mathrm{d}t} = -\gamma(v)\vec{v} + \vec{\omega} \times \vec{v} + \sqrt{2D_v}\,\vec{\xi}(t) \tag{2}$$

We assume that $\vec{r} = \{r_1, r_2\}$ and $\vec{v} = \{v_1, v_2\}$ are two-dimensional vectors, respectively, for the position and the velocity of the considered particle. D_v scales the randomness of the motion which is due to the stochastic sources in (2). Therein $\vec{\xi}(t)$ is a Gaussian stochastic force with unit strength, independent components and a δ-correlated time dependence

$$\left\langle \vec{\xi}(t) \right\rangle = 0\,, \qquad \langle \xi_i(t)\xi_j(t') \rangle = \delta_{ij}\,\delta(t - t'). \tag{3}$$

The new term in (2) is the Lorentz-like force which models the circular motion. We assume that $\vec{\omega}$ is directed perpendicularly to the plane of motion, i.e. $\vec{\omega} = \{0, 0, \omega\}$ and a Larmor-like rotation is generated. The sign of ω determines clockwise or counter clockwise motion. Later we will assume that half of a population is running clockwise and the second half counter clockwise.

The situation can be better understood if we change to polar coordinates in the velocity space by introducing

$$v_1 = v(t)\,\cos\left(\phi(t)\right)\,, \qquad v_2 = v(t)\,\sin\left(\phi(t)\right) \tag{4}$$

This change of variables is quite similar to an often used transformation in the phase space of nonlinear oscillators [21]. In contrast we consider a transformation within the two-dimensional velocity space.

The equations of motion transform into

$$\frac{\mathrm{d}v}{\mathrm{d}t} = -\gamma(v)\,v + \cos(\phi)\,\xi_1 + \sin(\phi)\,\xi_2 \tag{5a}$$

$$\frac{\mathrm{d}\phi}{\mathrm{d}t} = \omega + \frac{1}{v}\left(-\sin(\phi)\,\xi_1 + \cos(\phi)\,\xi_2\right). \tag{5b}$$

Without noise the velocity vector relaxes to a constant modulus $v = \sqrt{\alpha}$ which moves with constant angular frequency ω.

In Stratonovich-interpretation the corresponding Fokker-Planck equation for the density in the v, ϕ-space then follows [20, 22, 23]

$$\frac{\partial}{\partial t}P(v,\phi,t) = \frac{\partial}{\partial v}\left[\gamma(v)\,v - \frac{D_v}{v}\right]P - \omega\,\frac{\partial P}{\partial \phi} + D_v\,\frac{\partial^2 P}{\partial v^2} + \frac{D_v}{v^2}\,\frac{\partial^2 P}{\partial \phi^2}. \tag{6}$$

Its stationary distribution can be easily found

$$P_0\left(v,\phi\right) = N\,v\,\exp\left(-\frac{1}{D_v}\int \gamma(v)\,v\,\mathrm{d}v\right), \tag{7}$$

which is uniformly distributed in ϕ. We see that the rotational motion has no influence on the stationary density. We mention that the Larmor rotations are inducing a circulating probability flow. The most probable values can be easily found from (7)

$$\gamma(\tilde{v}) - \frac{D_v}{\tilde{v}^{\,2}} = 0\,. \tag{8}$$

In the limit of weak noise and strong pumping $D_v/\alpha \to 0$ we approximate the velocity distribution by a δ-function around the most probable values $(v \geq 0, \tilde{v} > 0)$

$$P_0\left(v,\phi\right) = \frac{1}{2\pi}\delta\left(v - \tilde{v}\right)\,. \tag{9}$$

3 Mean square displacement

We will characterize the motion of the active particles by its mean square displacement. In our case without external confinements the random motion induces linear diffusion in the long time limit at large length scales. Hence the mean square displacement is determined by the diffusion coefficient which is in two dimensions

$$\left\langle\left(\vec{r}(t) - \vec{r}(0)\right)^2\right\rangle = 4\,D_r\,t\,. \tag{10}$$

For a more detailed discussion of linear diffusion and the connected Einstein relations see [24, 25].

In order to calculate D_r we integrate the velocity, which yields

$$\vec{r}(t) = \vec{r}(0) + \int_0^t dt_1 \vec{v}(t_1). \tag{11}$$

Therein we agreed that the particles have been started at $t = 0$ in $\vec{r}(0)$. By this way the mean square displacement reads

$$\left\langle (\vec{r}(t) - \vec{r}(0))^2 \right\rangle = \int_0^t dt_1 \int_0^t dt_2 \left\langle \vec{v}(t_1) \vec{v}(t_2) \right\rangle, \tag{12}$$

and is traced by to the velocity correlation function. Crossing to radial and angle variables in velocity space (Eq.(4)) gives

$$K(t) = \left\langle \vec{v}(t_1) \vec{v}(t_2) \right\rangle = \left\langle v(t_1) v(t_2) \cos(\phi(t_1) - \phi(t_2)) \right\rangle. \tag{13}$$

Our main approximation is a widely used decoupling of $v(t)$ from the dynamics of the angle $\phi(t)$ [26]. Then for the correlation function we find

$$K(t) \simeq \left\langle v(t_1) v(t_2) \right\rangle \left\langle \cos(\phi(t_1) - \phi(t_2)) \right\rangle \tag{14}$$

More restrictively we require that the modulus of the velocities is approximately fixed which results in $\left\langle v(t_1) v(t_2) \right\rangle = \tilde{v}^2$ and $\tilde{v}$ is due to Eq. (8).

Hence the mean square displacement is due to the correlations of angles of the velocity vector. From Eq. (6) we get for the angle-distribution the Fokker-Planck equation

$$\frac{\partial}{\partial t} P(\phi, t) = -\omega \frac{\partial P}{\partial \phi} + D_\phi \frac{\partial^2 f}{\partial \phi^2} \tag{15}$$

with the diffusion coefficient $D_\phi = D_v / \tilde{v}^2$. Solving (15) with $t_1 > t_2$ gives

$$P(\phi_1, t_1 | \phi_2, t_2) = \frac{1}{\sqrt{4 D_\phi \pi (t_1 - t_2)}} \exp\left[-\frac{(\phi_1 - \omega(t_1 - t_2) - \phi_2)^2}{4 D_\phi (t_1 - t_2)} \right]. \tag{16}$$

This expression is used for averaging the cosine of the increment in angles $\phi(t_1) - \phi(t_2)$. Afterwards the time integrals can be calculated by standard calculations and a lengthy expression is obtained. We give here the long time asymptotic behavior where a linear increase becomes dominant over decaying and constant items. It has a simple shape as

$$\left\langle (\vec{r}(t) - \vec{r}(0))^2 \right\rangle = 2 \tilde{v}^2 \frac{D_\phi}{D_\phi^2 + \omega^2} t + O\left(\text{const}, \cos(\omega t), \exp(-D_\phi t) \right) \tag{17}$$

Hence the diffusion coefficient becomes

$$D_r = \frac{\tilde{v}^4}{2 D_v} \left(\frac{1}{1 + \omega^2 \tilde{v}^4 / D_v^2} \right). \tag{18}$$

The first factor agrees with an expression derived by Mikhailov and Meinköhn [27] in case there is no preference in the turning angle ($\omega = 0$). The second factor in the brackets decreases in case of $\omega \neq 0$. This solution for the spatial diffusion coefficient is in qualitative agreement with previous results based on a random walk model [17].

We point out that the diffusion coefficient does not depend on the sign of ω, hence not on the direction of rotations. Therefore the derived expression is true also if part of the population hops clockwise and the other part counter-clockwise.

The general dependence of the diffusion coefficient (18) on noise D_v and mean turning angle is shown in Figure 1. It decreases monotonically with the mean turning angle ω. Remarkable one finds a maximum with respect to the noise. It is located at noise values

$$D_v^{\mathrm{max}} = \tilde{v}^2 \, \omega. \tag{19}$$

and the spatial diffusion coefficient equals $\tilde{v}^2/4\omega$.

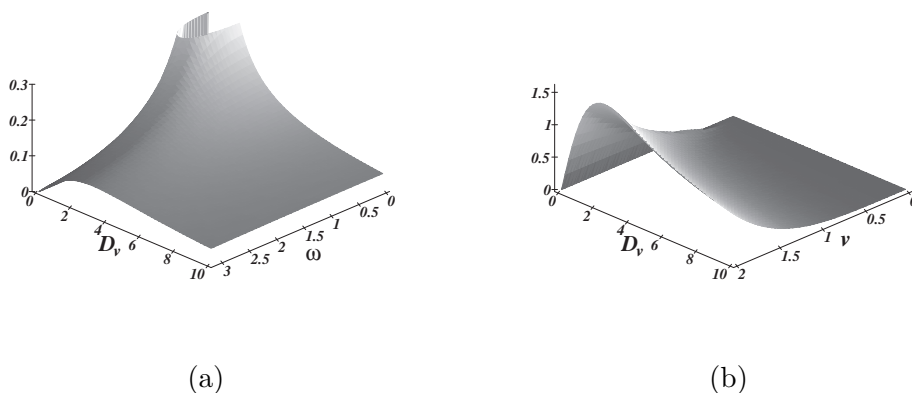
(a)   (b)

Fig. 1. Spatial Diffusion D_r depending on external noise D_v and the preferred turning angle ω (a) or the velocity v in the stationary case (b)

4   Optimal food consumption of finite food patches

In this section we want to develop a simple approach how much food a single *Daphnia* could consume while it is on its foraging path. Assuming that the density of the animal $\varrho(\vec{r}, t)$ obeys a diffusion equation with the afore-calculated

diffusion coefficient D_r

$$\frac{\partial \varrho}{\partial t} = D_r \Delta \varrho. \tag{20}$$

In two dimensions the resulting probability density in space is

$$\varrho(\vec{r}, t) = \frac{1}{4\pi \, D_r \, t} \exp\left[-\frac{\vec{r}^2}{4D_r t}\right]. \tag{21}$$

We assume that the particle during its random motion consumes with constant rate k food C which is given by its density $c(\vec{r}, t)$. If the food is un-movable in space, the consumption of food is described by the dynamics

$$\frac{\partial}{\partial t} c(\vec{r}, t) = -k \, c(\vec{r}, t) \, \varrho(\vec{r}, t) \tag{22}$$

The latter equation can be solved exactly if the solution (21) is inserted. Simple quadrature gives

$$c(\vec{r}, t) = c_0(\vec{r}) \, \exp\left[-\int_{t_0}^{t} k \, \varrho(\vec{r}, t') \, dt'\right]. \tag{23}$$

With the definition of the exponential integral [28], $\mathrm{E}_1(a) = \int_a^\infty \frac{e^{-t}}{t} dt$, we obtain in compact shape

$$c(\vec{r}, t) = c_0(\vec{r}) \, \exp\left[-\frac{k}{4\pi D_r} \, \mathrm{E}_1\left(\frac{\vec{r}^2}{4D_r t}\right)\right]. \tag{24}$$

where we have put $t_0 = 0$.

Let us look at bounded distributed food patches now. As a prototypical distribution we take spheres with radius R where C is present. Outside of the circle no food is located. For simplicity we assume the circle positioned at the origin, i.e.

$$c_0(\vec{r}) = c_0 \quad \text{if} \quad |\vec{r}| < R. \tag{25}$$

and vanishing, elsewhere. Then after a fixed time T we determine the overall food which is still left. It results from integration

$$C(T) = 2\pi \, c_0 \int_0^R \exp\left[-\frac{k}{4\pi D_r} \, \mathrm{E}_1\left(\frac{r^2}{4D_r T}\right)\right] r \, dr. \tag{26}$$

Inspection of this expression shows that there exists a minimum with respect to the diffusion coefficient D_r. Since D_r depends monotonously on the mean turning angle ω of the zig-zag hopping it implies a minimum with respect to the mean angle, too. Thus, the variation of the mean angle with change of the

effective diffusion coefficient gives rise to a change of the food consumption. One might speculate that nature has found by this way the reason to optimize the zig-zag hopping.

The consumed food as a function of the spatial diffusion coefficient D_r is shown in Fig.2. A simple explanation can be given as follows. If particles hop straight forwardly they will leave the food region, going forwardly and backwardly is also of disadvantage. Hence there is a optimal angle which the particle spends most time in the food patch with. It does not matter whether they start at the center of the food or not.
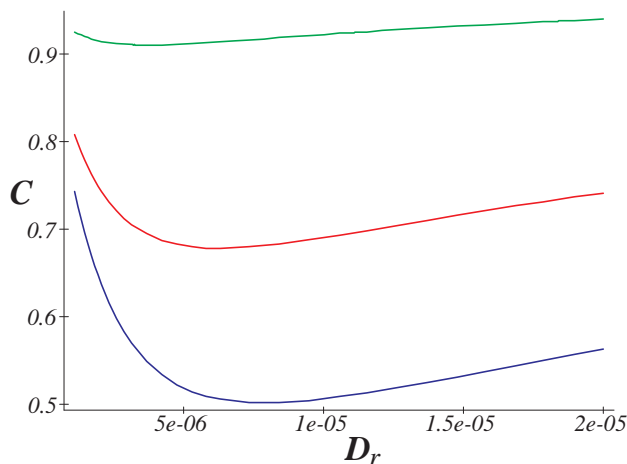

Fig. 2. Consumed food depending on the diffusion coefficient.

5   Conclusions

This paper extends the theory of Active Brownian particles with terms which obey the motion of individuals with preferred turning angle. This motion could have been observed, for example, in zooplankton populations like *Daphnia* [15]. The preferred turning angle distribution, which could have been easily put into a Random Walk model [17], comes into play as a Lorentz-like force within the Langevin equation. This translation of the preferred turning angle distribution into the concept of stochastic differential equations makes the treatment of such biological systems more handy in terms of physical interpretations of the influencing forces. With the help of the, now more generalized, theory of Active Brownian particles a broader variety of swarming systems can be described via physical models.

We calculated the spatial diffusion coefficient, and what is astonishing, is a

maximum of spatial diffusion with the noise strength for preferred turning angles $-\pi/2 < \omega < \pi/2$. The diffusion law (see Eq. (18)) is an extension of the theory presented in [27]. This result can be concluded as follows: With a preferred turning angle a individual can cover a larger area within a given time. This would be an evolutionary advantage as could have been seen in Sec. 4. Here we develop a theory of food consumption within a bounded food patch. Assuming a Gaussian distributed density for a single individual, and using the results from the sections before, a minimum in the left over food with the spatial diffusion coefficient has been found. Hence, to cover the maximum of a given area going zig-zag is many times more beneficial than just normal diffusion. Within a given time a individual can cover a bigger area with preferred turning angle and therefore consume more food, which is of evolutionary advantage.

Acknowledgements

References

[1] A. Einstein, M. v. Smoluchowski, Untersuchungen über die Theorie der Brownschen Bewegung, 3rd Edition, Vol. 199/207 of Ostwalds Klassiker der exakten Naturwissenschaften, Harri Deutsch, Frankfurt am Main, 1997.

[2] P. Langevin, C. R. Acad. Sci. (Paris) 146 (1908) 530–533.

[3] M. Schienbein, H. Gruler, Bull. Math. Biol. 55 (1993) 585–608.

[4] D. Helbing, P. Molnár, Phys. Rev. E 51 (1995) 4282–4286.

[5] W. Ebeling, F. Schweitzer, B. Tilch, BioSystems 49 (1999) 17–29.

[6] U. Erdmann, W. Ebeling, F. Schweitzer, L. Schimansky-Geier, Eur. Phys. J. B 15 (2000) 105–113.

[7] D. Helbing, Rev. Mod. Phys. 73 (2001) 1067–1141.

[8] A. S. Mikhailov, V. Calenbuhr, From Cells to Societies, Springer, Berlin, 2002.

[9] U. Erdmann, W. Ebeling, L. Schimansky-Geier, A. Ordemann, F. Moss, Active brownian particle and random walk theories of the motions of zooplankton: Application to experiments with swarms of *Daphnia*, http://arxiv.org/abs/q-bio.PE/0404018 (Apr. 2004).

[10] L. Schimansky-Geier, M. Mieth, H. Rosé, H. Malchow, Phys. Lett. A 207 (1995) 140–146.

[11] U. Erdmann, *Interjournal* Complex Systems (1997) 114.
URL http://www.interjournal.org/manuscript_abstract.php?10536

[12] D. Helbing, F. Schweitzer, J. Keltsch, P. Molnár, Phys. Rev. E 56 (1997) 2527–2539.

[13] C.-R. Sheu, C.-Y. Cheng, R.-P. Pan, Phys. Rev. E 59 (1999) 1540–1544.

[14] R. Mach, F. Schweitzer, in: W. Banzhaf, T. Christaller, P. Dittrich, J. T. Kim, J. Ziegler (Eds.), Advances in Artificial Life, Springer, Berlin, 2003, pp. 810–820.

[15] A. Ordemann, G. Balazsi, F. Moss, Physica A 325 (2003) 260–266.

[16] U. Erdmann, W. Ebeling, Fluct. Noise Lett. 3 (2003) L145–L154.

[17] N. Komin, U. Erdmann, L. Schimansky-Geier, Fluct. Noise Lett. 4 (2004) L151–L159.

[18] A. Okubo, S. A. Levin, Diffusion and Ecological Problems: Modern Perspectives, 2nd Edition, Springer, New York, 2001.

[19] J. W. S. Rayleigh, The Theory of Sound, 2nd Edition, Vol. I, MacMillan, London, 1894.

[20] R. L. Stratonovich, Topics in the Theory of Random Noise, Vol. II, Gordon and Breach, London, 1967.

[21] P. Hänggi, P. Riseborough, Am. J. Phys. 51 (1983) 347–352.

[22] V. S. Anishchenko, V. V. Astakhov, T. E. Vadivasova, A. B. Neiman, L. Schimansky-Geier, Nonlinear Dynamics of Chaotic and Stochastic Systems, Springer, Berlin Heidelberg, 2002.

[23] The afore-mentioned change of variables within the set of Langevin equations would be equivalent to a transformation within the Fokker-Planck equation derived from Eq. (2) [20, 24].

[24] P. Hänggi, H. Thomas, Phys. Rep. 88 (1982) 207–319.

[25] P. Hänggi, P. Talkner, M. Borkovec, Rev. Mod. Phys. 62 (1990) 251–342.

[26] P. Hänggi, P. Jung, Adv. Chem. Phys. 89 (1995) 239–326.

[27] A. S. Mikhailov, D. Meinköhn, in: L. Schimansky-Geier, T. Pöschel (Eds.), Stochastic Dynamics, Springer, Berlin, 1997, pp. 334–345.

[28] M. Abramowitz, I. A. Stegun, Pocketbook of Mathematical Functions, Harri Deutsch, Frankfurt/Main, 1984.